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# A CASE STUDY of a DOUGLAS-FIR TUSSOCK MOTH OUTBREAK and STAND CONDITIONS 10 YEARS LATER

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usda douglas-fir tussock moth • research & development program •

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- E R R A T A -

This is a corrected copy of figure 6, page 11, for USDA For. Serv. Res. Pap. PNW-244, "A Case Study of a Douglas-fir Tussock Moth Outbreak and Stand Conditions 10 Years Later," by Boyd E. Wickman.

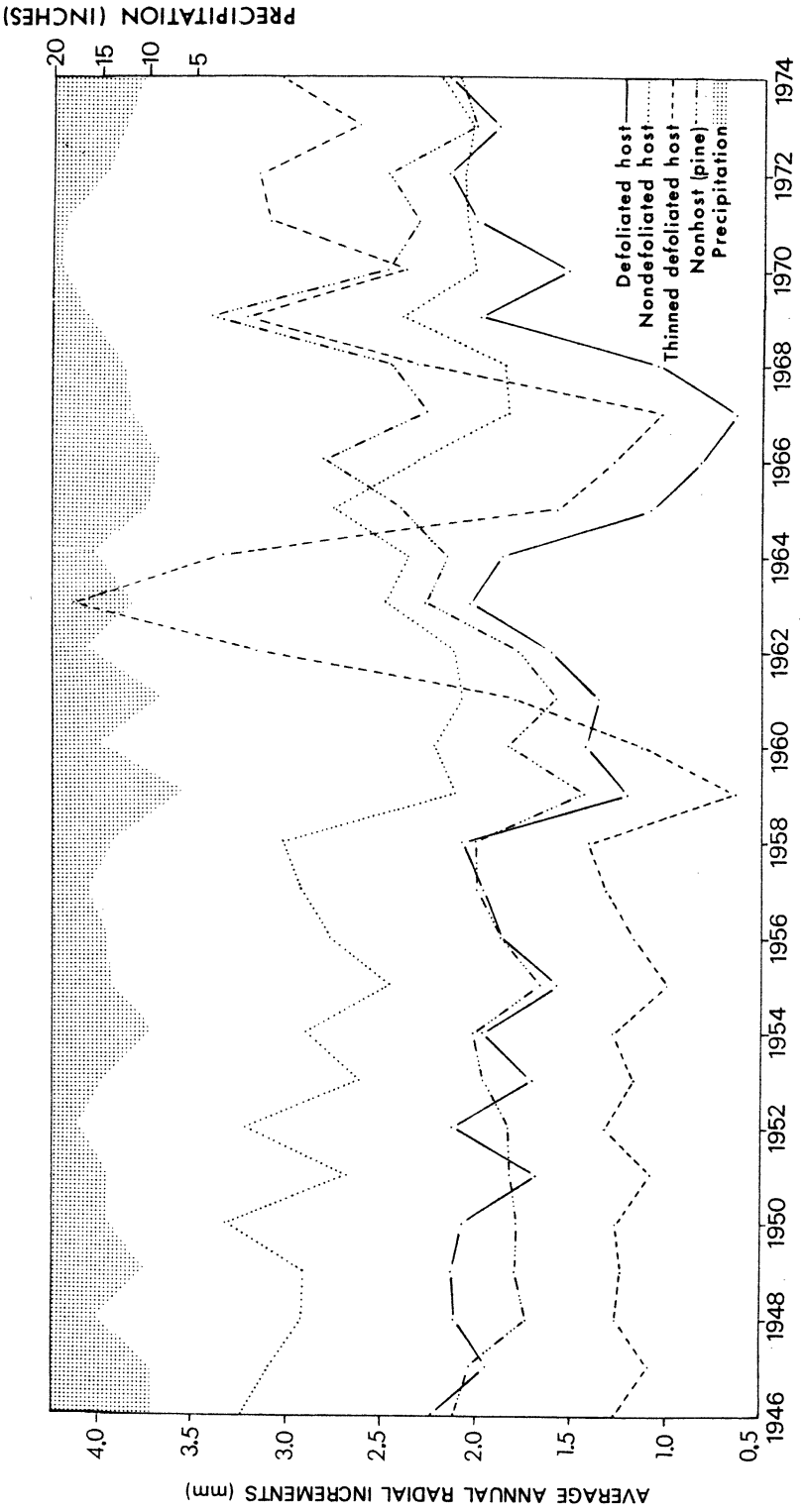



Figure 6.—Average annual radial increment at d.b.h. comparison of hosts and nonhosts, Stowe Reservoir, and annual precipitation, Cedarville.

# A Case Study of a Douglas-fir Tussock Moth Outbreak and Stand Conditions 10 Years Later

*Reference Abstract*

Wickman, Boyd E.
1978. A case study of a Douglas-fir tussock moth outbreak and stand conditions 10 years later. USDA For. Serv. Res. Pap. PNW-244, 22 p., illus. Pacific Northwest Forest and Range Experiment Station, Portland, Oregon.

Tree damage occurring immediately after an outbreak of Douglas-fir tussock moth, *Orgyia Pseudotsugata* McD., and stand conditions 10 years later are described. Because of increased radial growth and ingrowth in the 10-year postoutbreak period, good evidence indicates that tree damage caused by the tussock moth may not be as severe in the overall stand dynamics as previously pictured. The insect probably plays a key role as a phytophagous regulator of primary production in some second-growth white fir stands in California and elsewhere.

KEYWORDS: Insect damage (-forest, Douglas-fir tussock moth, *Orgyia Pseudotsugata*

*RESEARCH SUMMARY*
*Research Paper PNW-244*
*1978*

In early summer 1964, campers at the Stowe Reservoir campground were noticing and complaining about hairy little caterpillars dropping on their picnic tables and food. Campground garbage collectors a few weeks later complained that the abundant caterpillars gave them a rash when they dropped onto their bare arms or necks. Local Forest Service personnel investigated and found defoliation on many fir trees. They immediately requested help from regional office entomologists, who identified the hairy little caterpillars (now quite a bit larger) as Douglas-fir tussock moth larvae, which were very rapidly devouring most of the foliage on white firs near the campground. In an emergency effort to control the insects in and around the campground, 200 acres were sprayed with malathion on August 2, 1964, with absolutely no effect on the population. By then the entire Stowe Reservoir basin of 450 acres had turned reddish brown from the feeding activity. An outbreak was obviously in progress—the results of that outbreak and what followed are the subjects of this paper.

# Introduction

In 1964-65, the Douglas-fir tussock moth, *Orgyia pseudotsugata* McD., caused heavy defoliation of white fir, *Abies concolor* (Gord. and Glend.) Lindl., over thousands of acres of timber stands in northeastern California. Large patches of saplings and pole-size trees were completely stripped of needles. By late summer 1964, tree mortality was occurring on heavily defoliated areas in the largest recorded outbreak in California: 76,000 acres in five infestation centers. Stowe Reservoir was one of those infestation centers and, although the smallest, was the most intensely affected in the entire outbreak.[1]

In June and July 1965, 57,079 acres including 2,098 acres around Stowe Reservoir were aerially treated with 3/4 lb DDT in 1 gal of fuel oil per acre. The combined effects of the insecticide, a natural virus, and other natural enemies halted the outbreak. But tree damage of varying degrees was obvious over a wide area.

Because the infested area at Stowe Reservoir was small yet typical of a normal large outbreak in northeastern California, several studies were undertaken there on the development of egg mass sampling (Luck and Dahlsten 1967) and aerial photography techniques for sampling tree damage (Wert and Wickman 1968, 1970). The area was also visited 5 years after the outbreak to assess effects on the campground (Wickman and Renton 1975) and to make some measurements of tree mortality and growth. In 1975, the area was cruised for tree mortality, stand conditions, and tree growth in an attempt to duplicate the ground measurements of a 1967 aerial photography study (Wert and Wickman 1970). The objective of this paper was to see what kind of stand mortality, tree growth, and ingrowth prevailed on a seriously damaged outbreak area 10 years later. The effects of the outbreak have also been reported in summary fashion (Wert and Wickman 1970, Wickman et al. 1973). This paper describes the stand conditions before the outbreak, damage immediately after the outbreak, and conditions 10 years later. Because of the intensive research efforts in the area to date and its maintenance by the Modoc National Forest in an undisturbed state, I hope that additional studies will be carried out in future years.

[1] Unpublished mimeographed report, "Douglas-fir tussock moth infestations in northern California, 1964," by John R. Pierce. USDA For. Serv. Reg. 5, Div. Timber Manage., San Francisco, Calif. December 14, 1964.

# Study Area

Stowe Reservoir (fig. 1) is 1 mile (1.6 km) east of Cedar Pass on Highway 299 in the Warner Mountains of Modoc County, California. The Warner Mountains are an isolated range lying north-south about 100 miles (160 km) long. The south portion, about 60 miles (97 km), is in California just east of Alturas; the remainder extends into Oregon. The range is in the form of a tilted block, with a steep slope along the fault on the east side. Elevations over 9,000 ft (2 750 m) occur, but the crest of the range averages 7,000 to 8,000 ft (2 220 to 2 450 m). Cedar Pass is the lowest pass and bisects the range in the middle of the California portion. The west flanks of the Warner Mountains are heavily timbered with pine and fir. Stowe Reservoir is on the drier, east flank where timber grows in scattered patches along with sagebrush and juniper.

The 1964-65 tussock moth infestation occurred on 450 acres (182 ha) in a moderately sloping basin with mainly south and east exposures. The elevation ranges from 5,600 to 6,200 ft (1 700 to 1 900 m) with higher elevations and rocky escarpments immediately to the north and west. The second-growth stand is predominantly white fir with a scattering of ponderosa pine, *Pinus ponderosa* Laws., Washoe pine, *P. washoensis* Mason and Stockwell, and western juniper, *Juniperus occidentalis* Hook., at the lower elevations and southern exposures.

**Figure 1.—Location and area of white fir type killed by defoliation from the Douglas-fir tussock moth at Stowe Reservoir. The map was produced from the 1:8,000-scale color photography.**

The original stand was heavily logged about the turn of the century and the stumps show that a pine stand of large trees (36- to 40-in d.b.h.) covered all but the upper elevations. It was logged a second time for fir overstory in all but the campground area in 1954. No fires have burned in the stand for at least 50 years and probably none since the turn of the century. White fir is now the predominant tree species, growing as scattered patches of saplings, poles, and young sawtimber throughout the basin.

# Methods

Numerous examinations have been made of the outbreak since 1967 to obtain various bits of information, for example damage to the campground (Wickman and Renton 1975), but only the major study efforts will be recorded here.

In 1967, as part of an aerial photography study, a crew systematically sampled the area by examining conditions on 1/50th-acre (0.008-ha) circular plots, established at 2-chain intervals along cruise lines 5 chains apart (Wert and Wickman 1970). Small-scale (1:8,000 ft) aerial photographs were used to determine cruise lines. Large — scale (1:1,500 ft) aerial photo coverage and data from the plots provided an estimate of pre-outbreak stand conditions and total white fir damage in the area. A 1.5-percent sample of the area or 5.7 acres (2.3 ha) of plots were established to obtain a coefficient of variation

of 15 percent of the number of green and dead trees. On each plot, the following were recorded: d.b.h. of all trees 1-in and larger; tree species; crown condition (alive, dead, thin, normal, and length of top-kill, if present); year and cause of death; and white fir regeneration (alive and dead). Standard volume tables were used to compute volume of green and dead trees.

In 1975, using the same small-scale aerial photographs to establish cruise line locations, we repeated the examinations. We tried to duplicate the techniques used in 1967 as closely as possible to determine stand conditions 10 years later. One difference occurred, however, because of an error in the Wert and Wickman (1970) publication. That publication states that 1/40th-acre (0.01-ha) plots were used, but the original study plan and files[2] containing data calculations state the plot size as 1/50th acre. The plot size was set at 1/40th acre, as stated in the publication. We consequently carried out the 1975 cruise with slightly larger plots, ending with a larger sample: 279 plots or 7 acres (2.8 ha) of sample. The only effect of increased plot size would be to increase precision of the later sample.

We also took radial-growth measurements in 1975 (additional samples were taken in 1977) to determine stand growth and changes in growth patterns. Two increment cores were taken at breast height on each dominant or codominant tree nearest the plot center on every third plot. Cores were also taken from pine on about every eighth plot, from non-defoliated white fir 0.4 km south of the highway, and defoliated white fir in two plots thinned in 1960.

Some information on the level of tree mortality in the patches of severe defoliation scattered through the outbreak was obtained in 1970. A 100-percent cruise was made of five patches of tree mortality.

[2]Now filed at Rocky Mt. For. and Range Exp. Stn., Fort Collins, Colo.

In 1969 we destructively sampled five white fir with known 1965 defoliation levels by cutting discs at breast height, midcrown, and 17 internodes from the terminal. My inferences are restricted to this specific geographic locality; however, within it, statistical tests (regression analysis and t-tests) were applied to certain classes of trees. Stand characteristics were compared by stratifying individual 1/50th-acre plots into stand classifications. When characteristics of individual trees are examined statistically, I am assuming independent random sampling of trees even though trees occur in clusters by plots.

# Results

A summary of the green-stand statistics is given in table 1 for 1964, preoutbreak; 1967, 2 years postoutbreak; and 1975, 10 years postoutbreak. Calculations of damage and recovery that follow are based on these figures.

## TREE MORTALITY

Most of the mortality was caused by the effects of defoliation alone (table 2). Little mortality was caused by fir engraver beetle (*Scolytus ventralis* Lec.) in weakened trees. And most of the mortality occurred in 1964-65 and then tapered off the next 2 years. During the 1975 cruise, we attempted to back-date mortality to see if we could estimate losses from tussock moth after 10 years and also to see if losses were continuing. Tree death can be back-dated fairly accurately for about 2 years; so table 3 presents reliable tree mortality data by year and cause for 1973 to 1975. Cause and amount of outbreak mortality is difficult to identify accurately after 10 years, but apparently little bark beetle activity continued after 1967. In 1973 a general increase of this type of tree mortality occurred in white fir throughout the Warner Mountains.

*Table 1—Green-stand white fir and ponderosa pine (larger than 1-inch d.b.h.) at Stowe Reservoir, 1964-1975*

| Year | Per acre | | | | | | |
|---|---|---|---|---|---|---|---|
| | Living trees | | Basal area | | Volume[a] | | D.b.h. |
| | No. | S.E. | $F^2$ | S.E. | Fbm | S.E.[b] | average (in) |
| White fir | | | | | | | |
| 1964 | 331 | 19 | 193.2 | 10.8 | 13,101 | 1,077 | 8.8 |
| 1967 | 220 | 13 | 142.0 | 8.7 | 9,857 | 823 | 9.3 |
| 1975 | 240 | 16 | 132.4 | 7.6 | 11,013 | 912 | 7.7 |
| Ponderosa pine | | | | | | | |
| 1964 | 19 | 3 | 19.5 | 2.9 | 1,482 | 235 | 12.9 |
| 1967 | 18 | 3 | 18.6 | 2.8 | 1,422 | 231 | 12.8 |
| 1975 | 17 | 3 | 16.0 | 2.6 | 1,424 | 290 | 11.2 |

[a]International 1/4-in rule—trees 10.0-in d.b.h. and larger to a 6-in top diameter inside bark.
[b]Standard error of mean determined from individual-plot data.

*Table 2—White fir mortality by year and cause, Stowe Reservoir, 1964-67, (based on 1,889 trees alive in 1964)*

| Year | Tussock moth | | Bark beetle | | Tussock moth & bark beetle[a] | | Other | |
|---|---|---|---|---|---|---|---|---|
| | No. | % | No. | % | No. | % | No. | % |
| Pre-1964 | 0 | 0 | 0 | 0 | 0 | 0 | 4 | 0.2 |
| 1964[b] / 1965 | 528 | 28.0 | 2 / 15 | 0.9 | 0 | 0 | 1 / 7 | 0.4 |
| 1966 | 12 | 0.6 | 48 | 2.5 | 4 | 0.2 | 4 | 0.2 |
| 1967 | 0 | 0 | 7 | 0.4 | 3 | 0.2 | 2 | 0.1 |
| Total | 540 | 28.6 | 72 | 3.8 | 7 | 0.4 | 18 | 1.0 |

[a]Not certain which killed the tree.
[b]Not certain of year of death.

*Table 3—White fir mortality by year and cause, Stowe Reservoir, 1973-75 (based on 1,725 trees living in 1973)*

| Year | Tussock moth | | Bark beetle | | Other | |
|---|---|---|---|---|---|---|
| | No. | % | No. | % | No. | % |
| 1973 | 0 | 0 | 16 | 0.9 | 1 | 0.1 |
| 1974 | 0 | 0 | 25 | 1.5 | 5 | 0.3 |
| 1975 | 0 | 0 | 3 | 0.2 | 1 | 0.1 |
| Total | 0 | 0 | 44 | 2.6 | 7 | 0.5 |

White fir mortality was stratified by diameter classes, based on the 1967 data (fig. 2). Most of the loss caused by tussock moth occurred in the 1- to 6-in d.b.h. class, but the small amount of mortality caused by bark beetle steadily increased up to the 19- to 24-in d.b.h. class. Trees larger than 24-in d.b.h. suffered no loss from bark beetles on our plots.

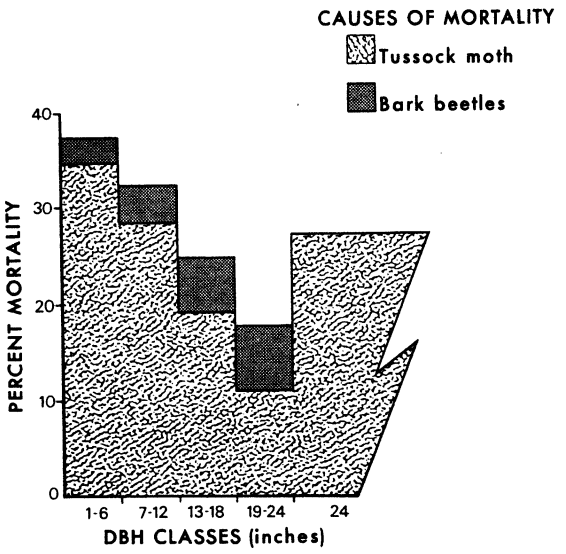



**Figure 2.—Percent mortality of white fir by d.b.h. classes, Stowe Reservoir, 1967.**

A summary of stand statistics from the 1967 cruise is given in table 4. From these data we calculated that 28.6 percent of the stand (number of trees) and 20.6 percent of the stand volume were killed by the tussock moth in this heavily defoliated outbreak area. When bark beetle mortality was added, about 32 percent of the stand volume was killed. Tree mortality was also summarized (table 5) for advanced reproduction (trees below 1 inch in diameter but more than 10 years old) and recent regeneration (trees less than 10 years old). This information was compared for the 1967 and 1975 cruises to show the amount of mortality caused by tussock moth and amount of postoutbreak regeneration and ingrowth for these size classes. Mortality has been high among advanced reproduction since 1967, even without defoliation. Most of these trees were suppressed and over-topped so the recent high mortality was probably caused by competition. From the difference between 1967 losses (29 percent) and 1975 losses (20 percent), I infer that only 9-percent mortality was caused by tussock moth in this class. In any case, in-growth of this size class has resulted in more trees per acre in 1975 than were present before the outbreak.

Regeneration-sized trees apparently suffered 34-percent mortality from tussock moth, but by 1975 the total number of white fir regeneration-size trees was equal to preoutbreak levels. Most of this regeneration was 6 to 9 years old, indicating a rapid reestablishment of white fir seedlings. The largest concentrations of regeneration were found in the patches of 1965 tree mortality.

## PATCHES OF TREE MORTALITY

The data from the five patches of severe tree mortality cruised in 1970 are summarized

*Table 4—Summary of 1967 white fir stand conditions per acre*

| Item | Mean/acre | S.E. |
|---|---|---|
| Number of live trees | 220.4 | 13.1 |
| Basal area | 142.0 | 8.7 |
| Number of dead trees | 111.8 | 10.6 |
| Number killed by tussock moth | 94.9 | 9.8 |
| Volume[a] live | 9,857 | 823 |
| Volume[a] dead (includes bark beetle caused mortality) | 3,347 | 567 |
| Volume[a] killed by tussock moth | 2,688 | 523 |

[a]Board feet, Scribner International Rule.

*Table 5—Survival and mortality of white fir regeneration by year and size (age) class*

| Year | Trees per acre | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Advance reproduction | | | | | | Regeneration | | | | | |
| | Living | | | Dead | | | Living | | | Dead | | |
| | No. | S.E. | % | No. | S.E. | % | No. | S.E. | % | No. | S.E. | % |
| 1967 | 7.20 | 1.85 | 70.6 | 3.00 | 1.40 | 29.4 | 85.61 | 9.85 | 65.9 | 44.21 | 6.75 | 34.1 |
| 1975 | 43.36 | 4.84 | 79.8 | 10.96 | 2.84 | 20.2 | 129.75 | 25.33 | 98.7 | 1.72 | .93 | 1.3 |

1967—44% of 1/50th-acre plots have regeneration.
1975—36% of 1/40th-acre plots have regeneration.

*Table 6—Sample of five patches of white fir severely damaged by Douglas-fir tussock moth, 1964-1967*

| Patch no. | Size (acres) | Dead trees/acre (no.) | Live trees/acre (no.) | Total trees/acre (no.) | Mortality/acre (percent) |
|---|---|---|---|---|---|
| 1 | 2.5 | 305 | 85 | 390 | 78.2 |
| 2 | 5.75 | 369 | 24 | 393 | 93.9 |
| 3 | 1.0 | 224 | 58 | 282 | 79.4 |
| 4 | 3.5 | 259 | 55 | 314 | 82.5 |
| 5 | 4.0 | 319 | 61 | 380 | 83.9 |
| Total | 16.75 | 1,476 | 283 | 1,759 | |
| $\bar{x}$ | 3.4 | 295.2 | 56.6 | 351.8 | 83.9 |
| S.E. | | 25.0 | 9.7 | | |

*Table 7—Top-kill determined during the 1967 cruise, by percent of top-kill in various d.b.h. classes*

| D.b.h. class | Percent of crown top-killed | | | | |
|---|---|---|---|---|---|
| | 1-10 | > 10 | Total | Other top-kill | |
| Inches | | | Percent | | |
| 0-6 | 5.3 | 0.4 | 5.7 | 0 | |
| 7-12 | 10.1 | 6.2 | 16.3 | 2.2 | |
| 13-18 | 6.1 | 12.5 | 18.6 | 1.0 | |
| 19-24 | 5.6 | 13.9 | 19.5 | 0 | |
| > 24 | 0 | 0 | 0 | 0 | |
| All trees | 7.3 | 5.1 | 12.4 | 1.0 | 13.4 total |

in table 6. The average size of these patches was 3.4 acres, and they contained 295 dead trees per acre (83.9 percent of the stand). All patches of tree mortality of 1 acre or larger in the outbreak were delineated on the aerial photos and measured with a dot grid. From this measurement, I estimated that this type of damage occurred on about 8 percent of the area—37 acres of the 450 acres mapped as outbreak. When calculated on the basis of 270 net acres of white fir type within the 450 gross acres, then patches of tree mortality occurred on 14 percent of the timbered area.

## TOP-KILL

In 1967 only three classes of top-kill were used to record this type of damage. They were 1-10 percent of the crown killed, greater than 10 percent, and older or top-kill unrelated to tussock moth. Top-kill data are summarized in table 7. The greatest amount of top-kill (7.3 percent) occurred in the 1 to 10 percent of the crown category, followed by those trees with greater than 10 percent of the crown top-killed (5.1 percent). Total top-kill attributed to defoliation was 12.4 percent, similar to the 12 percent found in an earlier California outbreak (Wickman 1963), but less than found in the Blue Mountains outbreak (Wickman 1978).

Top-kill was also tallied during the 1975 cruise, but six classes were used. They were: leader-only (not attributed to tussock moth at this late date); 1 to 10 percent of the crown killed; 11 to 25 percent; 26 to 50 percent; greater than 50 percent; and other older top-kill (fig. 3). Perhaps only a portion of the

Figure 3.—Percent top-kill of white fir by d.b.h. classes for Stowe Reservoir, 1975.

top-kill was outbreak related, but we wanted to see if an increase of top-kill incidence or severity might be attributed to 1964-65 defoliation. The 1975 data were combined into the three classes used for 1967 data, with leader-only top-kill included in the "other" category not caused by tussock moth (table 8).

An interesting finding is that total top-kill in the stand dropped from 13.4 percent in 1967 to 7.0 percent in 1975, and this included leader-only damage (1.6 percent) which we did not tally in 1967. The probable reason for the decline in top-kill was that more top-killed trees died during the interval from 1967 to 1975 than non-top-killed trees. Some evidence suggests that top-killed trees are more susceptible to mortality by bark beetles (Wickman 1963 and 1978). No explanation has been found for the leader-only damage, but light-to-moderate defoliation by Modoc budworm (*Choristoneura viridis* Freeman) occurred in the area in 1974 and 1975.

## FOLIAGE CONDITION

Foliage condition categorized subjectively as being "normal" or "thin" was estimated for each tree for both cruises. We did this because we did not have any defoliation estimates for individual trees and thought that the thin-foliage trees were probably the most severely defoliated in 1964 and 1965. A check of this condition 10 years later in 1975 could give some indication of foliage recovery. These data were summarized for both cruises by diameter classes to see if some effect was related to tree size (table 9).

The data suggest several relationships. First, most of the thin-foliage trees in 1967 occurred in the 1- to 6-in and 7- to 12-in d.b.h. classes, indicating either more severe defoliation in those classes or slower foliage recovery 2 years after the outbreak. Second, 2 years after the outbreak over half the trees look normal in foliage complement. And third, 10 years after the outbreak 98 percent of the trees appear to have normal foliage complements with most of the thin-foliage trees remaining in the 1- to 6-in d.b.h. class. Some of these trees may have been categorized thin because they were suppressed understory.

## GROWTH

Growth was measured after the outbreak by both destructive sampling and increment cores. The analysis presented here can be

*Table 8—Top-kill determined during the 1975 cruise, by percent of top-kill in the various d.b.h. classes*

| D.b.h. class | Percent of crown top-killed | | | | |
|---|---|---|---|---|---|
| | 1-10 | > 10 | Total | Other top-kill | |
| Inches | ——————————Percent—————————— | | | | |
| 0-6 | 0.6 | 0.8 | 1.4 | 3.1 | |
| 7-12 | 2.1 | 1.8 | 3.9 | 2.9 | |
| 13-18 | 2.1 | 4.8 | 6.9 | 1.9 | |
| 19-24 | 4.3 | 5.4 | 9.7 | 10.8 | |
| > 24 | 0 | 3.0 | 3.0 | 5.9 | |
| All trees | 1.4 | 1.8 | 3.2 | 3.8 | 7.0 total |

*Table 9—Foliage condition of white fir by d.b.h. class 1967 and 1975*

| D.b.h. (in) | Foliage condition | | | |
|---|---|---|---|---|
| | Normal | | Thin | |
| | No. | % | No. | % |
| 1967 | | | | |
| 1-6 | 225 | 48 | 243 | 52 |
| 7-12 | 245 | 49 | 251 | 51 |
| 13-18 | 157 | 71 | 64 | 29 |
| 19-24 | 51 | 86 | 8 | 14 |
| > 24 | 8 | 100 | 0 | 0 |
| Total | 686 | 55 | 566 | 45 |
| 1975 | | | | |
| 1-6 | 836 | 97 | 22 | 3 |
| 7-12 | 433 | 99 | 4 | 1 |
| 13-18 | 255 | 100 | 0 | 0 |
| 19-24 | 83 | 100 | 0 | 0 |
| > 24 | 32 | 100 | 0 | 0 |
| Total | 1,639 | 98 | 26 | 2 |

broken down into immediate, short-term patterns of growth reduction and 10-year postoutbreak effects.

*1. Short-term patterns of reduction (immediate postoutbreak).*—In early spring 1965, 100 trees were given defoliation estimates, using the scheme of percent of crown lengths totally defoliated, reported for the Blue Mountains outbreak (Wickman 1978). In 1969, five of these trees were felled and destructively sampled with a disk cut at breast height, midcrown, and about 17 internodes from the terminal. The defoliation levels for each tree were: one tree, 50-percent, and four trees, 75-percent defoliated. Figure 4 shows the radial growth averages for these heavily defoliated trees. They all showed some growth reduction starting in 1964, a drastic reduction for the years 1965-67, and recovery to preoutbreak growth by 1969. Top and midcrown growth was reduced more than at

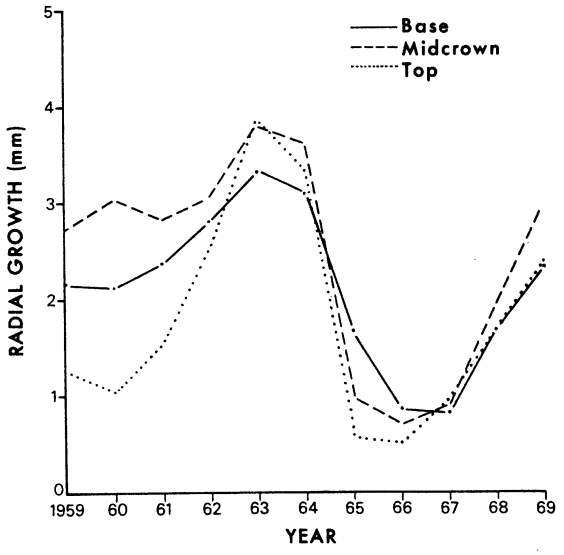



**Figure 4.—Average radial growth at base, midcrown, and top for five heavily defoliated white fir, Stowe Reservoir.**

the base of trees for 2 years following defoliation. Height growth was also measured on seven additional small trees in heavy defoliation class (50-percent or more defoliated) and seven small trees in the light class (less than 50-percent defoliated). These measurements are shown in figure 5 and follow a pattern similar to radial growth except growth reduction started in 1964 at a pronounced rate and recovery was a year earlier than for radial growth.

The data presented are based on such small samples that it is useful only as an illustration of patterns of growth reduction immediately after defoliation. These patterns are similar to those studied previously (Wickman 1963).

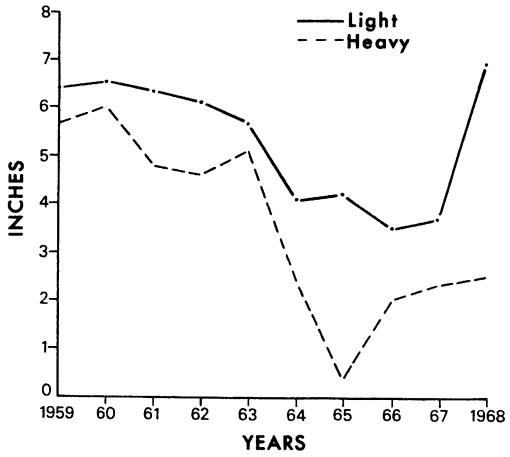



Figure 5.—Average annual height growth for 12 heavily and 7 lightly defoliated white fir, Stowe Reservoir.

*2. Ten-year postoutbreak growth patterns.*— Growth patterns for the 10-year postoutbreak period were obtained from the following sets of trees: defoliated white fir on the plots, 116 trees; nonhost pine on the plots, 36 trees; defoliated white fir from two plots thinned in 1960, 35 trees—thinned areas were 1.2 and 0.6 acres (.49 ha and .24 ha) and spacing was irregular, but averaged 25 by 25 ft (7.6 m); and nondefoliated white fir, 35 trees. Average radial growth for the period 1946-1974 from each of the four sets of trees is shown in figure 6. The annual precipitation from the station in Cedarville, California, about 15 miles (24 km) east is plotted at the top of the figure. The normal 13 inches (33 cm) per year is the average from 1940 to 1971. The values for 1956 and 1957 were estimated, because of unavailable data, from values at Alturas, California, the next closest station.

Data on the nondefoliated white fir and the pine trees in figure 6, show that the same yearly growth responses are exhibited but the amplitude of the trends are different. The radial growth trend of the nondefoliated white fir is toward a gradual decline. The nonhost, ponderosa pine, exhibits increased growth from 1964 to 1969. In part, the increased growth during this period might be explained by the natural thinning effect and increased nutrient and water supply during and immediately after the tussock moth outbreak. The trends change in 1969 when the pine begins to decrease; the nondefoliated fir decreases slightly and then remains static.

The growth trends of the defoliated white fir and the defoliated, thinned white fir exhibit patterns similar to the first two sets but only until 1960. The stand representing the thinned host was thinned during 1960, and it expressed an unusually high growth-response peak in 1963. This peak was similar to that found by Seidel (1977) in suppressed grand fir released by killing the overstory lodgepole pine. Growth reduction resulting from defoliation in 1964-65 was similar for both thinned and unthinned white fir. Post-outbreak growth in thinned plots, however, has been at a higher level than in unthinned white fir.

The depression of growth for all trees in 1959, 1961, 1973 appears related to precipitation deficiencies during those periods. The subnormal precipitation from 1965 to 1967 is of particular interest because it confounds the effects of defoliation on growth reduction. Defoliation obviously depressed growth in 1965 and 1966, but the 1967 reduction

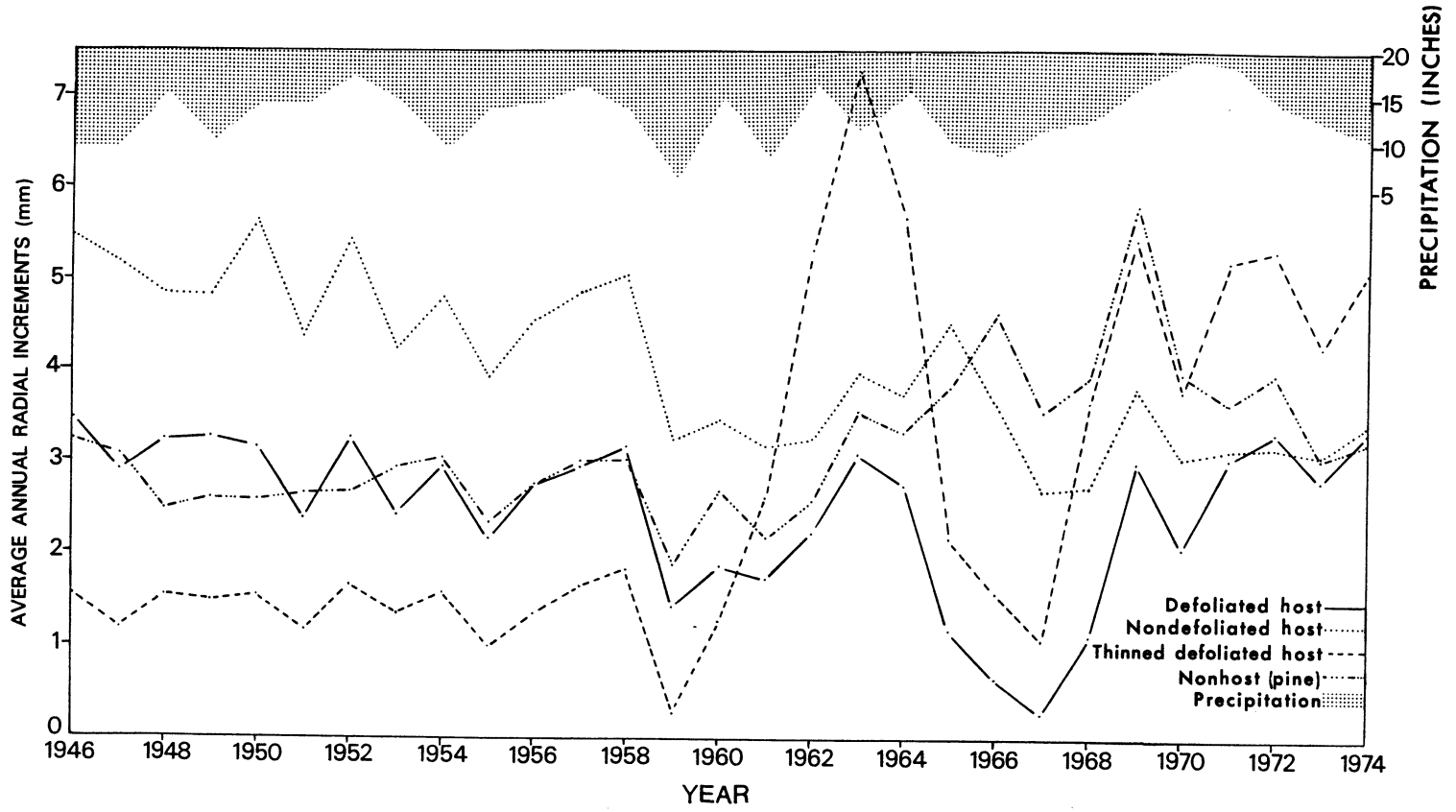



Figure 6.—Average annual radial increment at d.b.h. comparison of hosts and nonhosts, Stowe Reservoir, and annual precipitation, Cedarville.

probably would not have been as severe or recovery might have occurred a year earlier without several years of subnormal precipitation during the critical, postoutbreak recovery period. This points out the complexities in assessing the effects of defoliation on growth and the fallacy of assigning all growth reduction in the defoliated trees to the tussock moth outbreak.

The growth depression in 1970 for all trees is an unexplained anomaly, because it occurred during a period of above-average precipitation. It could have been related to effects of combinations of temperature and precipitation occurring in one or several seasons of the year. It does indicate that tree-growth patterns are complex and often unexplainable because we lack information on the interrelationships of tree physiology with environmental factors in a given locality and time.

Some comparisons were made of average radial growth for the four classes of trees during 6 preoutbreak years of 1959-1964, the 4 outbreak and immediate postoutbreak years of 1965-1968, and 6 postoutbreak years of 1969-1974. Each of the periods has 2 years of depressed growth from environmental effects, and the thinned host has the additional effect of mechanical reduction of stand density in 1960. Paired t-tests were then made to compare growth within each of the four tree classes during these periods.

Growth of defoliated host was significantly reduced (at the .01 level) during and immediately after the outbreak (1965-68) compared to growth in the preoutbreak and postoutbreak periods (table 10). The surprising growth relation for defoliated host is that of the 6-year postoutbreak period. Even in this short time, defoliated-host growth is significantly greater (at the .01 level) than during a similar preoutbreak period. Nondefoliated host shows no significant growth differences among all three periods indicating that environmental effects were not unduly affecting growth in any one period. The thinned, defoliated host was similar to the defoliated host except that preoutbreak growth was significantly higher (at the .05 level) than postoutbreak growth. This was probably because of very high growth in 1962 and 1963 as an immediate response to mechanical thinning.

The nonhost (pine) growth was significantly greater (at the .01 level) during the outbreak and postoutbreak periods compared to the preoutbreak period.

Another comparison of growth rates using regression analysis was conducted to test whether a linear relation exists between pre- and postoutbreak growth and whether the relations differ among classes. The relations of preoutbreak (1959-1964) to postoutbreak growth (1969-1974) were determined from individual trees, sampled as clusters on the plots, for each of the four classes (fig. 7a-d). The results of that analysis follow:

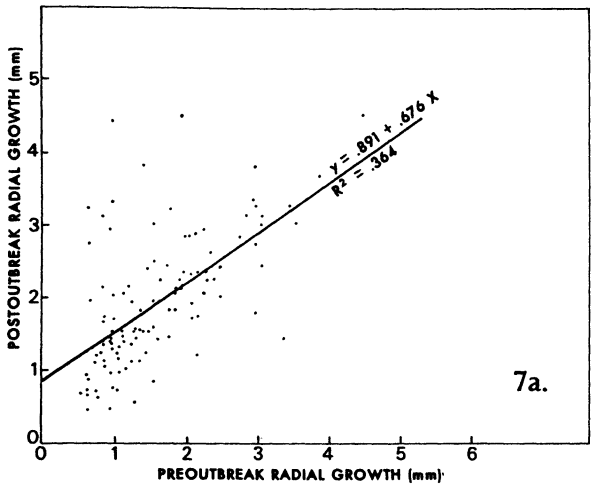
| | $R^2$ | F-value | Significance |
|---|---|---|---|
| Defoliated host | .36 | 65.20 | .01 |
| Nondefoliated host | .84 | 176.80 | .01 |
| Nonhost (pine) | .59 | 49.36 | .01 |
| Thinned, defoliated host | .06 | 1.99 | N.S. |

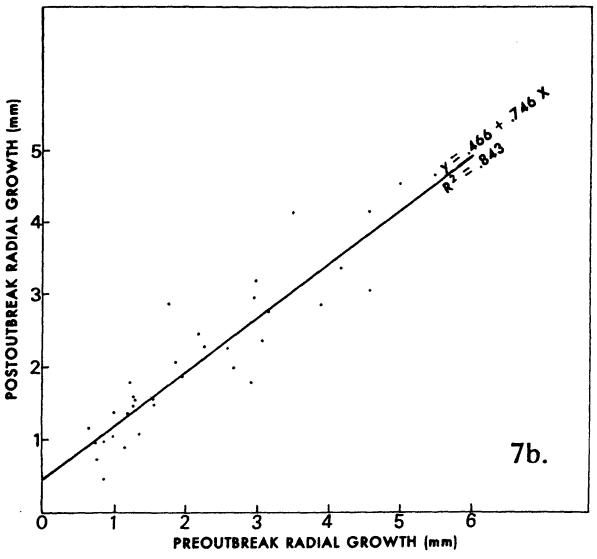
The slopes and intercepts of the significant regression lines were compared using an analysis of covariance (Snedecor and Cochran 1967) to determine if the classes had different relations. In comparing these regression lines in pairs, individual nonorthogonal contrasts are used. Because of the exploratory nature of this study, these comparisons were considered adequate. Figure 7e presents the regression lines for the four classes of trees. Using an F-test for difference between regression coefficients, the slopes of defoliated host, nondefoliated host, and nonhost were all found to be similar. This indicates that growth relations were similar for the three classes.

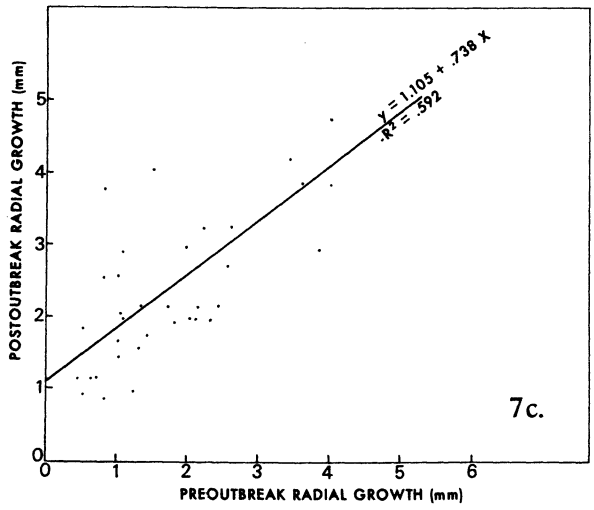
*Table 10—Comparisons of average growth in four tree classes during preoutbreak, outbreak, and postoutbreak periods using paired t-tests*

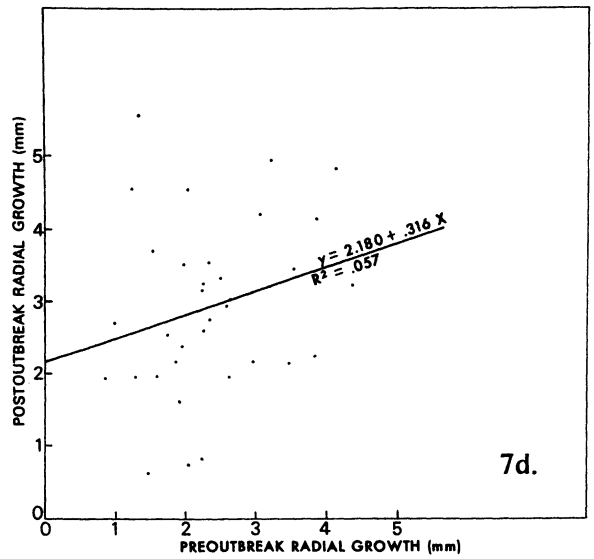
| Tree class | Means of radial growth | | | |
|---|---|---|---|---|
| | 1946-1958 | 1959-1964 | 1965-1968 | 1969-1974 |
| Defoliated host | 1.961 | 1.594 | 0.908 | 1.968 |
| Nondefoliated host | 2.927 | 2.242 | 2.197 | 2.138 |
| Thinned, defoliated host | 1.222 | 2.380 | 1.569 | 2.932 |
| Nonhost (pine) | 1.890 | 1.853 | 2.493 | 2.472 |

| | Growth periods | |
|---|---|---|
| | Preoutbreak (1959-1964) with outbreak (1965-1968) | |
| | T-value | Significance |
| Defoliated host | 12.173 | .01 |
| Nondefoliated host | .665 | N.S. |
| Thinned, defoliated host | 6.219 | .01 |
| Nonhost | 6.477 | .01 |
| | Preoutbreak (1959-1964 with postoutbreak (1969-1974) | |
| Defoliated host | 5.210 | .01 |
| Nondefoliated host | 1.108 | N.S. |
| Thinned, defoliated host | 2.505 | .05 |
| Nonhost | 4.856 | .01 |
| | Outbreak (1965-1968) with postoutbreak (1969-1974) | |
| Defoliated host | 14.650 | .01 |
| Nondefoliated host | .681 | N.S. |
| Thinned, defoliated host | 7.330 | .01 |
| Nonhost | .258 | N.S. |



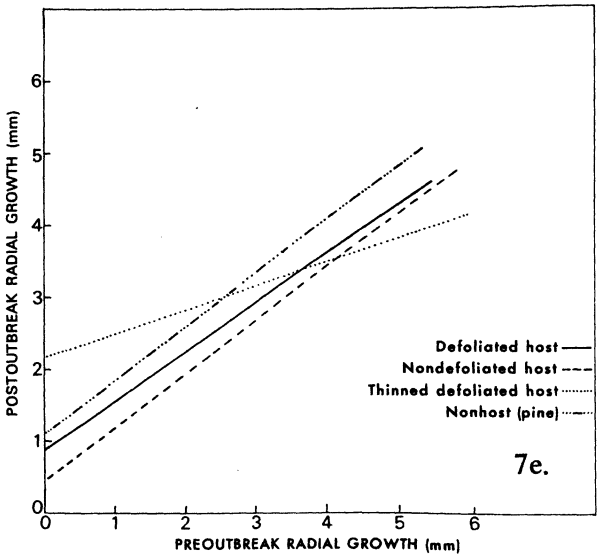




Figure 7.—a, Defoliated host radial growth; b, nondefoliated host radial growth; c, nonhost (pine) radial growth; d, thinned defoliated host radial growth; e, comparison of preoutbreak radial growth with postoutbreak growth.

Testing for differences in intercept showed a significant difference (.05 level) in the post-outbreak growth rate for nonhost (pine) over defoliated host and for both pine and defoliated host over nondefoliated host. In other words, both classes of trees in the infested area have responded with significantly greater growth rates in the 6-year postoutbreak period than nearby nondefoliated white fir, which remained fairly constant. This implies that postoutbreak growth increases in the outbreak area were probably not unduly influenced by environmental factors.

## PINE/WHITE FIR RELATIONS

Investigators have noted for many years that tussock moth outbreaks, especially the centers of highest populations and defoliation, have often been located on ridge tops or south slopes (Wickman 1963, Wickman et al. 1973). These locations are usually the most xeric sites in mountainous areas, and the tree species growing there often reflect this relation. In California, most outbreaks have occurred in mixed conifer stands, and in Modoc County most outbreaks have been in mixed pine-fir stands. Sometimes the overstory is pine and the understory fir (Mason and Thompson 1971). Southwood (1966) suggests several methods for measurement of association between species, particularly comparisons of two faunas. We applied one of the suggested tests, a 2 by 2 contingency tabulation, to two species of plants, pine and fir. The first tabulation is drawn to obtain a quantitative measure of the association of pine on plots containing white fir.

B. Pine[3] A. Number of plots with white fir

| | Present | Absent | Total |
|---|---|---|---|
| Present | a = 57 | b = 3 | 60 |
| Absent | c = 178 | d = 47 | 225 |
| | 235 | 50 | 285 |

[3]Such a tabulation should be drawn so that A is more abundant than B.

(ad - bc) = 2145 or a positive association.

A chi-square test was made where $\chi^2 = 7.205$, indicating a positive association which was not the result of chance or an interaction between the two species.

Because pine and fir are broadly intermixed throughout much of the infestation, this statistic does not tell us much. We are particularly interested in those areas where defoliation was severe enough to cause tree mortality. So a second tabulation was drawn comparing plots with white fir mortality associated with pine.

B. Pine A. Plots with white fir mortality

| | Present | Absent | Total |
|---|---|---|---|
| Present | a = 41 | b = 19 | 60 |
| Absent | c = 89 | d = 136 | 225 |
| | 130 | 155 | 285 |

A similar test produces $\chi^2 = 14.67$ and a positive association that was not the result of chance.

This implied relation of pine with centers of severe defoliation and tree mortality was pursued further by comparing the percent white fir mortality on blocks of sample plots with percent pine. Figure 8 shows the arrangement of blocks of plots used for the analysis. Blocks were divided on the basis of topography (elevation) and equal numbers of plots as closely as possible. An average of 32 plots was in each block; block number 9 had only 16 plots because of its unusual configuration. A regression analysis (fig. 9) indicates a positive correlation of pine and white fir mortality ($R^2 = .895$ significant at the .01 level). The correlation shows an interesting trend and indicates that highest tree mortality occurred on the sites supporting the most ponderosa pine. These are probably the driest ones where fir grows in this area.

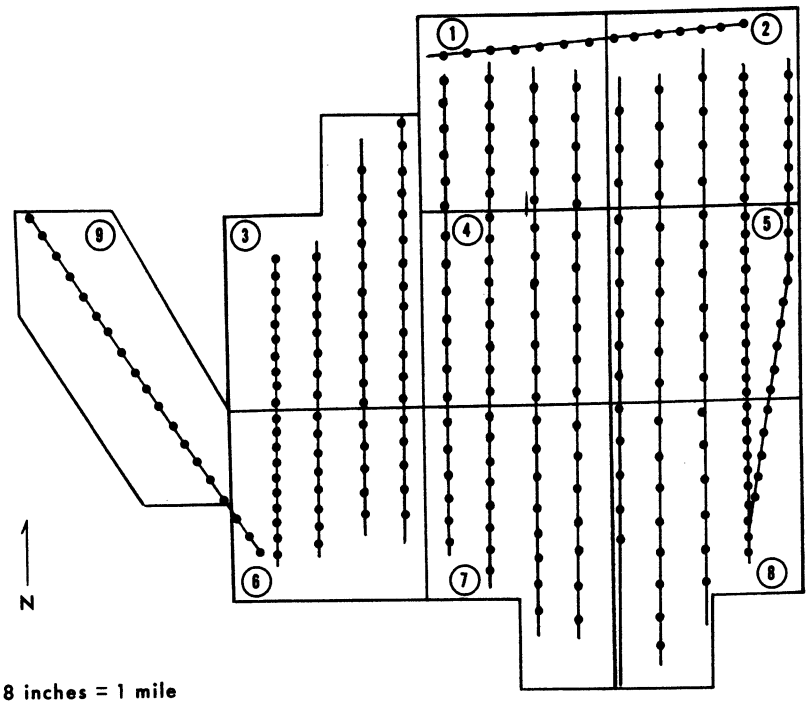



Figure 8.—Blocks of sample plots, arranged with nearly equal numbers of plots, used to compare white fir mortality with presence of pine.

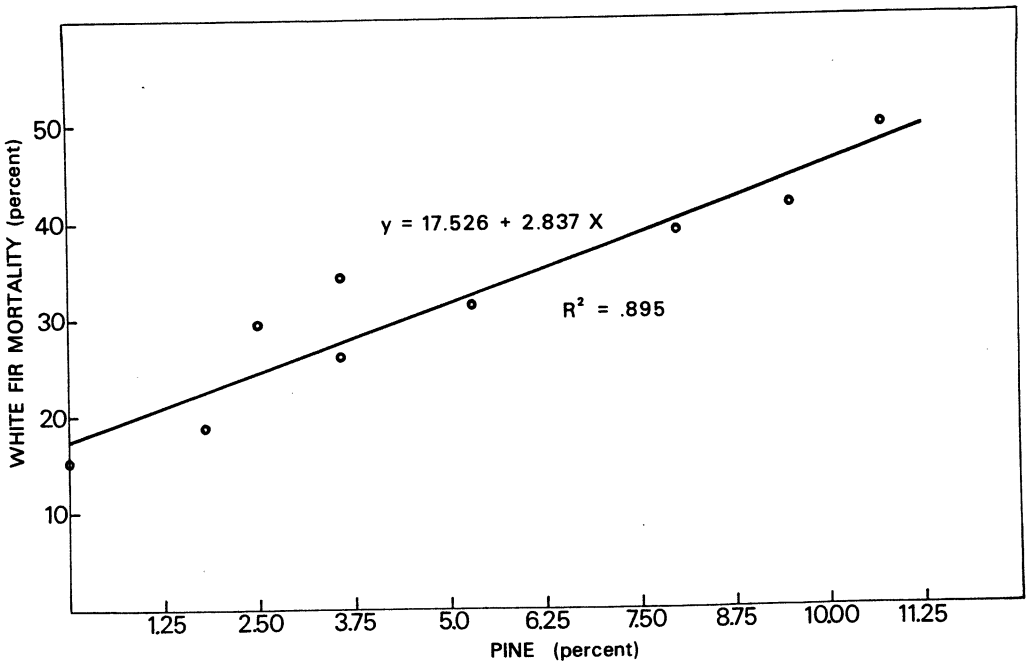



Figure 9.—Relation of white fir mortality to percentage of ponderosa pine in plots.

## TREE SPECIES COMPOSITION

The outbreak area contains four conifer tree species: white fir, ponderosa pine, Washoe pine (very similar to ponderosa pine), and western juniper. An examination of possible changes in overstory species composition in the short-term (10-year) period was attempted by comparing the standard plant ecology parameters of density, dominance, and frequency. The following results and conclusions are descriptive and are not based upon statistical analysis. Relative values for each were then obtained by the following formula:

$$\text{Relative density} = \frac{\text{density for a species}}{\text{total density for all species}} \times 100$$

Table 11 presents these values for 1964 (preoutbreak), 1967 (immediate postoutbreak), and 1975 (10 years postoutbreak). Surprisingly, little change appears for white fir and pine in the "relative" values, especially as white fir suffered 32-percent stand mortality in 1964-1967. The largest change in the 10-year postoutbreak period is with western juniper, where relative values triple.

The relative values for density, dominance, and frequency are sometimes combined into an "importance" value, which reflects the importance of the species in the community (Lindsay 1956). The importance value is determined by the formula:

Importance value = relative density + relative dominance + relative frequency.

*Table 11—Composition of white fir, pine, and western juniper for 1964, 1967, and 1975 based on living trees*

| Factor | Tree | 1964 | 1967 | 1975 |
|---|---|---|---|---|
| | | ——— Number ——— | | |
| Density (number per acre) | White fir | 331.4 | 220.4 | 239.9 |
| | Pine | 18.8 | 18.1 | 16.6 |
| | Juniper | 2.1 | 2.1 | 6.7 |
| Dominance (basal area per acre) | White fir | 193.2 | 142.0 | 132.4 |
| | Pine | 19.5 | 18.6 | 16.0 |
| | Juniper | 1.0 | 1.0 | 2.1 |
| Frequency (number of plots occurrence/total plots) | White fir | 82.5 | 79.6 | 81.0 |
| | Pine | 21.1 | 20.4 | 21.9 |
| | Juniper | 3.5 | 3.5 | 12.5 |
| | | ——— Percent ——— | | |
| Relative density | White fir | 94.1 | 91.6 | 91.1 |
| | Pine | 5.3 | 7.5 | 6.3 |
| | Juniper | 0.6 | 0.9 | 2.5 |
| Relative dominance | White fir | 90.4 | 87.9 | 88.0 |
| | Pine | 9.1 | 11.5 | 10.6 |
| | Juniper | 0.5 | 0.6 | 1.4 |
| Relative frequency | White fir | 77.0 | 76.9 | 70.2 |
| | Pine | 19.7 | 19.7 | 19.0 |
| | Juniper | 3.3 | 3.4 | 10.8 |

The importance values for the three species are calculated below to show the relations quantitatively.

**Importance Values**

| | 1964 | 1967 | 1975 |
|---|---|---|---|
| White fir | 261.5 | 256.4 | 249.3 |
| Pine | 34.1 | 38.7 | 35.9 |
| Juniper | 4.4 | 4.9 | 14.7 |

The importance-value decline for white fir was caused by tree mortality in 1964-67. The decline for the pine from 1967 to 1975 is suspected to be from a sampling error. The reason for the increased value for juniper in 1975 is unknown; it too may be an artifact of the sampling technique, or it could represent a delayed response to the outbreak. It was not caused by ingrowth, however, because most of the juniper were 6-in or larger d.b.h.

# Discussion

Obviously severe defoliation by the Douglas-fir tussock moth can cause heavy tree mortality. All of the outbreaks that have been studied to date, however, have exhibited a common pattern. Namely, mortality tends to be concentrated in patches that range in size from several to several hundred acres, depending on the size of the outbreak. The mortality occurring in these patches is severe, averaging about 84 percent of the trees; and the end result, even if the trees are salvaged to negate the economic loss, is a scattering of understocked chunks of land with loss of potential future growth. This also results in the added costs of adjusted timber management plans. The total area of these scattered patches is relatively small, however, usually 10 to 14 percent of the outbreak area. Perhaps half of the additional tree mortality occurs as scattered single trees and small groups in the area surrounding the patches. This scattered mortality may be viewed as a short-term loss if salvage is not possible; however, over a rotation period, a reduction in stand density probably has positive values by lessening tree competition and enhancing growth of survivors. For instance, 10 years after the outbreak, our measurements of advance reproduction showed only a 9-percent reduction from the immediate postoutbreak period. And regeneration counts (seedlings less than 10 years old) were back to the preoutbreak level 10 years later. Fye and Thomas (1963) found that 15 years after a spruce budworm outbreak, balsam fir and spruce seedlings released by the outbreak were growing so rapidly that they were retarding the height growth of some reproduction. And Ghent et al. (1957) showed that balsam fir seedlings responded to killing of the overstory with a fivefold increase of height growth. Growth of released reproduction, however, was only twice as great as under suppressed conditions before the outbreak. He concluded that the spruce budworm is itself a mechanism for release of established seedlings and affects the next forest no differently than other disturbances like cutting and fire.

Top-kill is usually negative in small trees, because it prevents their growing into well-formed crop trees. Surprisingly, on this area trees top-killed by tussock moth gradually disappeared, probably from mortality by bark beetles. If the disappearance of top-killed trees is part of the normal attrition within a stand, it may be improper to categorize all this loss as damage done by defoliation.

The economic effects of short-term growth loss are extremely difficult to quantify because of the many extrinsic factors affecting growth, particularly precipitation and tree competition.

Apparently the effect of defoliation on growth of white fir was of short duration. The effects of tree mortality reducing competition and possibly the nutrient cycling of insect frass and damaged needles during the outbreak has resulted in significantly greater

growth of both host and nonhost trees (especially the slower growing trees) during the postoutbreak period. Surprisingly, a positive growth trajectory has developed within a 6-year period. An important aspect is, of course, how long this relation will continue. The average age of defoliated white fir was 79 years and of nondefoliated pine, 92 years. If a conservative rotation period of 120 years is assumed, will accelerated growth of host and nonhost for another 30 to 40 years plus ingrowth of smaller trees then compensate for growth loss of the host alone during the outbreak? The answer to this question obviously needs continued study, but the implication of beneficial thinning effects of outbreaks in stand dynamics is intriguing and deserves further consideration.

This mixed bag of losses and gains from defoliation leads one to ask, "What is the role of the Douglas-fir tussock moth in western fir forests?" Here is a native insect, which has adapted to survival in a forest type that is rapidly undergoing changes caused mostly by man. If recent large outbreaks in British Columbia and the Pacific Northwest are indicative of a trend, then these man-caused changes may be creating conditions more susceptible to large outbreaks. Because we cannot look at the insect system separately from the forest system, I propose that there are several processes going on in the forest before, during, and after an outbreak that indicate the tussock moth is either a precursor to drastic successional changes or at least an indicator of unstable forest systems.

First, if one agrees with the hypothesis of Mattson and Addy (1975) and others that phytophagous insects are regulators of forest primary production, then the Douglas-fir tussock moth is a classic example of such a cybernetic regulator. The characteristics of insects acting as such a regulator as defined in Van Emden (1973) are as follows: They affect a plant's primary site of energy and biochemical synthesis by consuming foliage; several species of phytophagous insects are usually coextensive with a plant species so the plant almost always has an ubiquitous consumer (e.g., the Douglas-fir tussock moth, the Modoc budworm, and various loopers on white fir); and a long history of association and coevolution between insect and host has occurred.

As Mattson and Addy point out, this implies that insects, as regulators, can and do respond to changes in condition of the host, and the host-plant systems react and change both as individual trees and in stands to changes in their insect consumers. For instance, Kimmins (1972) has suggested that defoliations contribute additional nutrients to the soil. And Assmann (1970) claims that the weakened, old, and suppressed plants that usually die after defoliation result in more available nutrients, light, heat, and moisture for the survivors. Loucks (1970) goes a step further and says that drastic, natural, periodic disturbances are necessary every 50 to 100 years to return plant communities to an earlier successional stage, which affects species diversity and primary production. Taken together and given the lately increased understanding of plant ecosystems, lends credance to the concept that the tussock moth is playing a natural and, in the long term, beneficial role as a system regulator. This brings me to my second point: the effect of the host-plant system on the insect.

Over my 22 years of association with tussock moth outbreaks, I have observed an increasing tendency of outbreaks to occur in second-growth fir stands, often in association with pine. Sometimes the pine occurs as a definite overstory as in the Corral Creek, California, outbreak (Mason and Thompson 1971). The results of the study reported here are also intriguing in the association with pine. My hypothesis is that because of man's management practices over the past 75 years or so of harvesting overstory pine and excluding fire, we have favored an increase in the proportion of white fir on pine sites, thus creating vast acreages of susceptible host

stands throughout the West. Many of these stands are on xeric sites which are also apparently most suitable for the development and outbreak of tussock moth populations.[4] These successional patterns have been recorded by many foresters, and Franklin and Dyrness (1973) neatly summarized the condition for pine/fir sites in eastern Oregon similar to those in northeastern California. In short, periodic fires in the past helped maintain ponderosa pine stands. Fire control over the last 75 years has, in more moist sites, resulted in the replacement of ponderosa pine with white fir. This process has probably been speeded up wherever man logged pine from the stand.

Enter the tussock moth: the severe, though localized, outbreaks in California in 1936-37 and 1955-56 caused heaviest damage in old-growth, mixed-conifer stands. Since that time, outbreaks in California have occurred mostly in second-growth or undergrowth stands of white fir, usually in association with ponderosa pine. This relation has also been observed in the Blue Mountains of Oregon and Washington (Wickman 1978), although serious damage centers also occurred in old-growth stands of pure grand fir. And Stoszek (1977) notes that in recent Idaho outbreaks grand fir in stands with high-graded pine overstory suffered the greatest defoliation.

There are more influences on the development of outbreaks than exclusion of fire, high-grading pine, or increased host acreage on xeric sites. The responses of the tussock moth to foliage quality are probably very important (Beckwith 1976). Southwood (1973) contends that plant foliage is only marginally adequate nutritionally for insect consumers, and these consumers will react to small biochemical changes in plants caused by aging, fluctuations in soil moisture, pollution, or other stresses. The effects of weather on populations should also be considered. Morris (1963) has indicated that several summers of dry, warm weather appear to facilitate outbreaks of spruce budworm. Subnormal precipitation was noted for several years before two tussock moth outbreaks in California (Wickman 1963).

Also to be considered are the influences of a large array of natural enemies of the tussock moth. We know very little about their role in "releasing" outbreaks or possibly in preventing them in certain stands exhibiting favorable environmental conditions for the natural enemies. Research of this type under way may provide valuable leads for understanding these relations.[5]

Possibly recent changes in host stands are causing changes in host-plant quality and quantity that could also be influencing the habitats of natural enemies including the tussock moth and thus their responses to their hosts. These changes combined with the influences of weather on insect, natural enemies, and host could, in turn, result in large and damaging tussock moth outbreaks.

If we can accept the natural role of the tussock moth in, or as a result of, our new and changing forests, then perhaps we should look at the insect in a new light. Maybe the tussock moth is doing us a favor, by pointing out the fallacy of some of our forest management practices and acting as a regulator in an unstable system that we have created over vast acreages.

I don't mean to imply that wholesale conversion of fir/pine forests to pine will solve the problem. The bark beetle problems associated with unmanaged, second-growth stands of pine in the west are commonplace and of much greater magnitude than losses caused by Douglas-fir tussock moths. The principle of pest control by host management has been suggested by many as a solution to problems with defoliating insects; however, as pointed out by Baskerville (1975) for the

[4] R. R. Mason, USDA For. Serv., For. Sci. Lab., Corvallis, Oreg., personal communication.

[5] T. R. Torgersen and R. R. Mason, USDA For. Serv., For. Sci. Lab., Corvallis, Oreg., personal communications.

spruce budworm, some serious problems limit implementation. I do suggest that the risk of future Douglas-fir tussock moth outbreaks, at least in white fir forests, could probably be lessened by changes in our silvicultural practices.

One thing is heartening—the Douglas-fir tussock moth does not destroy entire white fir forests in California and rarely decimates Douglas-fir forests elsewhere. Patches of trees may be severely defoliated and die on some of the outbreak areas; additional scattered tree mortality occurs and this is probably beneficial in terms of thinning the stand. For several years after an outbreak growth may decline, but recovery is usually dramatic. Forests are remarkably resilient, and even man has to work hard at devastating one. Stowe Reservoir is a case in point. Man-caused disturbances have included: logging twice, exclusion of fire, heavy sheep grazing before 1900, continued cattle grazing, building of roads and recreation facilities, and spraying with malathion in 1964 and DDT in 1965. In contrast, the one major natural disturbance on record is the 1964-1965 tussock moth outbreak. Did it hurt the forest? Did it help the forest? I wish I could be around in 2065 to cruise the Stowe Reservoir outbreak area and find out.

# Acknowledgments

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